PATTERNS OF FORAGING AND METHODS OF SUSTAINABILITY IN HARVEST TREE SELECTION OF *ATTA COLOMBICA*, A PROPOSAL

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Summary: Herbivory can impact the community composition and ecosystem structure of forests. Leaf-cutting ants (*Atta colombica*) account for 42 % of herbivory in neotropical forests, and are generally thought to be selective foragers (Stevens 1983, Chen et al. 1997). But there are different plausible patterns of foraging that have different consequences. Ants could forage in a way that maximizes colony growth and reproduction in the short term, even if it depletes its food resources and limits colony lifespan, or ants could forage in a way that is sustainable in the long term. We propose a set of simple long-term measurements that will discriminate between these competing hypotheses, and could be conducted by future FSP groups with about one day of effort per year. Results will enhance our understanding of the complex effects of ants on tropical forests. For example, ants could become habituated to feeding on the few common tree species, in which case ant foraging would tend to increase local diversity. Alternatively, ants could forage to avoid toxicity thresholds of all the various secondary metabolites that they encounter, in which case ant foraging would tend to reduce local tree diversity.

Key Words: ant colony, leaf cutter ants, optimal foraging strategy, primary forest, secondary forest

INTRODUCTION AND BACKGROUND

Herbivory can strongly influence the species composition and structure of tropical forests. Leaf-cutting ants, such as *Atta colombica*, are particularly important herbivores in neotropical forests, harvesting an estimated 4.78 tons of leaves • ha^{-1} • $year^{-1}$ (Mannan et al. 1996). Given this harvest rate, there is little doubt that how ants select and manage their food resources influences the forest community. Possibilities include direct impacts on the tree survival and indirect impacts on food resources for other herbivores and on the light regimes experienced by understory plants. Leaf-cutting ants are generally regarded as highly selective foragers (Stevens 1983; Grace et al. 1997), but their patterns of harvesting are poorly understood. It has been hypothesized that foraging behavior of *A. colombica* has been selected to maximize productivity of the fungal gardens on which ants depend for their food (Stevens 1983). Colonies of *Atta* sp. are estimated to persist for 7-20 years, but it is not known if colony longevity is influenced by depletion of food resources around nests.

Patterns of tree selection and overall foraging behavior likely represent the dominant mechanisms by which this species impacts the primary and secondary forests in which it is found. Preliminary studies at Corcovado National Park, Costa Rica, indicate that the pattern of trails used by these ants to transport leaf fragments between host trees and the nest provide a convenient basis for testing alternative hypotheses regarding the harvest pattern of *A. colombica*.

OBJECTIVES AND HYPOTHESES

Our objective is to describe leaf-cutting foraging patterns and to assess if leaf-cutting ant harvesting methods are sustainable. We offer the following possible hypotheses.

HOST PLANT PREFERENCES

Hypothesis 1: Leaf-cutting ants harvest plant species non-randomly. This general hypothesis has several possible sub-hypotheses that lead to contrasting predictions (Table 1; Figs. 1 and 2).

Table 1. Ants harvest in a fixed rank preferential order across colonies. Hypothetical colonies 1, 2, and 3, harvest species X over species Y, and species Y over species Z.

	Preference Rank	1	2	3
Colony				
1		X	Y	Z
2		X	Y	Z
3		X	Y	Z

H_{1a}: Ants harvest according to a fixed rank preference of host plant species.

P_{1a}: Under this hypothesis, all ant colonies will tend to exhibit the same preferences regardless of the relative abundance of host species in their environment.

H_{1b}: Ants harvest to keep the accumulated dose of each specific plant secondary metabolite below a toxicity threshold.

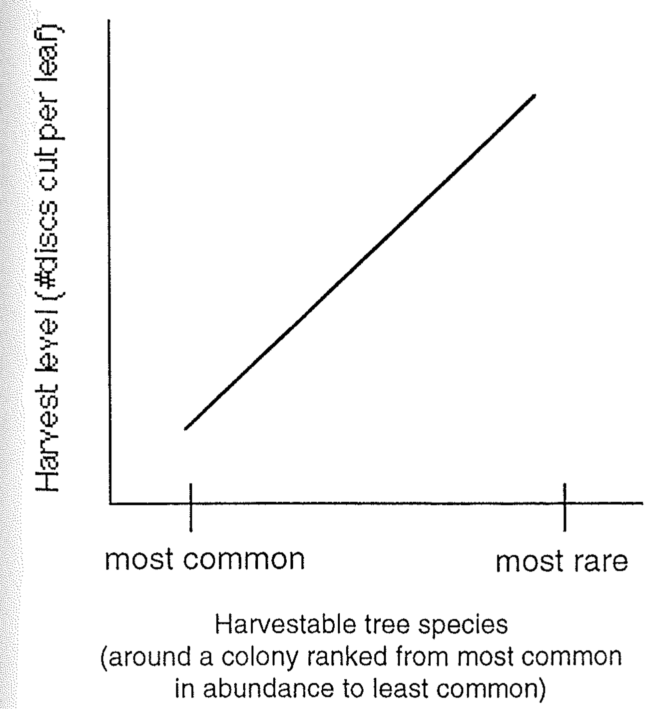

Figure 1. Possible results that would support the toxicity threshold hypothesis of ant foraging behavior (H1b). Under this hypothesis, ants favor the least consumed plant species because the ants are furthest from the toxicity threshold of secondary metabolites for that species.

P_{1b}: Under this hypothesis, preferences will change over time in a way that favors the selection of plant species that are relatively rare and disfavor species common in their environment.

P_{1b}: This hypothesis further predicts that ants should preferentially harvest species that the colony has recently consumed the least of because they will be furthest from the toxicity threshold for secondary metabolites produced by that species.

H_{1c}: Ants preferentially harvest tree species to which either the colony or the fungal symbionts are habituated.

P_{1c}: Under this hypothesis, ants will tend to favor the plant species on which they have already been feeding. Unlike H_{1b}, this hypothesis predicts that ants would benefit from harvesting more of the same species on which they

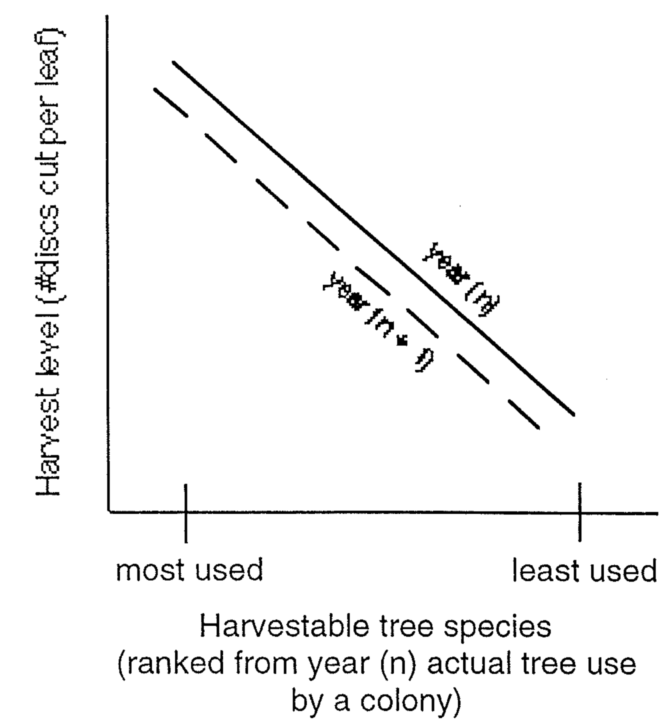

Figure 2. Possible results that would support the habituation hypothesis of ant foraging behavior (H1c). Under this hypothesis, colonies tend to harvest in year (n + 1) in the order that they harvested in year (n).

have already been feeding. This hypothesis predicts that different colonies could exhibit different preferences as compared with H_{1a}, which predicts the same preference rankings to occur across colonies.

We propose a set of simple preference assays that will provide a robust test of the hypothesis that ants harvest host species non-randomly and if the general hypothesis is supported, will distinguish among the three subhypotheses (see "Host Plant Preferences" in Methods; Table 1; Figs. 1-2).

Sustainability of harvesting

Hypothesis 2a: Leaf-cutting ants harvest the community of host plants surrounding their nest in a way that does not limit the lifespan of the colony (i.e., they harvest their host plants in a manner that is sustainable).

Hypothesis 2b: Leaf-cutting ants harvest in a way that maximizes colony size and reproduction in the short term even though this depletes local food resources and limits the potential longevity of the colony.

We propose to distinguish between these alternatives with a protocol of long term measurements to test for systematic increases in trail length and evaluate whether or not colonies with long foraging trails are more likely to become extinct (see "Sustainability of harvesting" in methods; Fig. 3-4).

Significance

Leaf-cutting ants comprise an estimated 42% of all herbivory in tropical forests (Mannan et al. 1996). Ant harvesting may impact the survival of tree communities, and the food resources available to other consumers in the forest ecosystem. Furthermore, because the tree species assemblages differ between primary and secondary forest, ant colonies in each habitat may have foraging strategies that affect these forest types differently. This project will provide the first systemic long-term studies of *Atta columbica* on the Osa Peninsula.

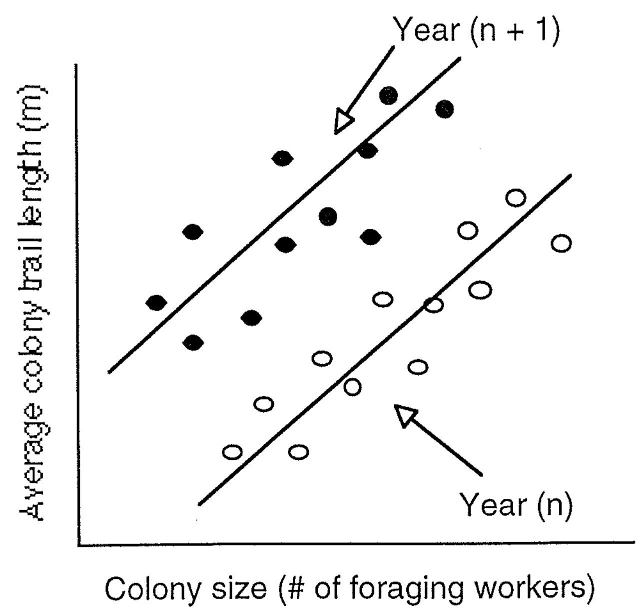

Figure 3. Possible results that would indicate that ants do not harvest their tree resources in a sustainable manner. Under this hypothesis, average trail length is expected to increase with age of a colony. These increases may be most evident when evaluated relative to colony size, which can be estimated by the number of foraging workers.

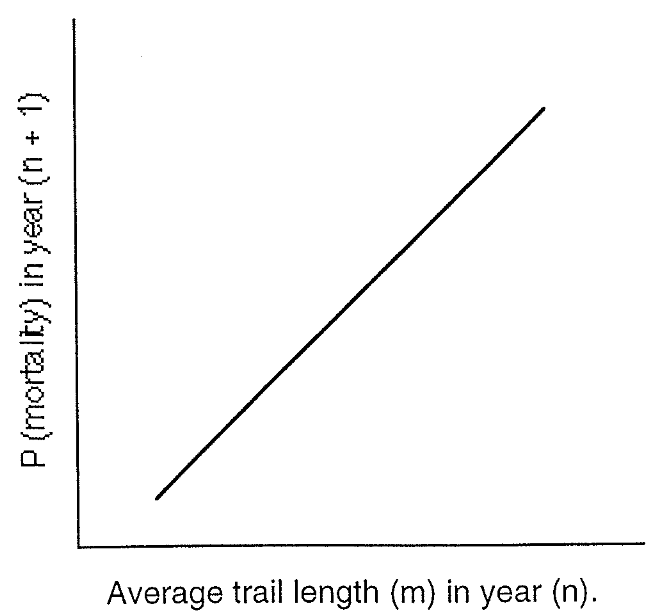

Figure 4. Possible results that would indicate that ants do not harvest their tree resources in a sustainable manner. Under this hypothesis, the probability of colony mortality increases with average trail length.

Methods

Life History and Study Site

Leaf-cutting ants, (*Atta colombica*) are present in lowland tropical forests throughout Costa Rica (Stevens 1983). Bands of individuals from the same colony travel on well-defined paths through the forest, collecting leaf fragments from host trees, and transporting the leaf material back to fungal food gardens located in the colony's communal nest (Stevens 1983). Each species of leaf-cutting ant maintains a single fungal species in their food garden (Chapela et al. 1994). Although fungal symbionts appear to be tolerant of a range of plant species, little is known about their precise species requirements. Leaf-cutting ants are extremely abundant at Corcovado National Park, Costa Rica. The park, located on the Osa Peninsula includes both primary and secondary forests.

Baseline Data

To measure colony survival and longevity, we will annually re-locate to nests that were mapped in 2000. For each previously surveyed colony, we will locate the focal point, defined as an arbitrarily marked tree near the ant colony that acts as a reference point to all landmarks, and then calculate the bearing and distance from the focal point to each hole and entrance. Next we will identify and count all active entrances (defined as mound entrances being used by ants to import leaves into the nest at time of sampling) and active trees (trees on which ants are foraging). We will record the distance between the 2 furthest entrances (length of mound), estimate the width of mound, and record all other holes (inactive and refuse).

We will also collect data on tree selection on a yearly basis. This will involve finding, mapping, and identifying trees that are currently being harvested. Each focal tree will be tagged at breast height (1.35 m) with a unique tag number (Tags will specify: secondary or primary forest, nest number, and tree number). Focal trees will be identified to the lowest taxonomic group possible. Because this is difficult to do in the field at Corcovado, it may be necessary to keep detailed descriptions of trees and/or photos of leaves to distinguish tree morphotypes. We will record the distance along the trail that leads from the active tree to the active entrance, find all trees and holes that were previously active, and record whether they are currently inactive or active (A sample data sheet is included in Appendix 1). Finally, we will create one inclusive scaled map of all trees, holes, and focal point. Included on the map will be the bearings and distances from the focal point to each landmark, as well as a reference tree that has been marked on the nearest trail. The reference trees will act as markers along the trail to facilitate relocation of each colony. A key for the map will include the following: entrance number, tree number, focal point and reference tree. We will take all of the above measurements once each year, at each of the previously surveyed colonies. To add newly active or newly surveyed colonies to the list of focal colonies, the above procedure will be followed at each new mound. Baseline data from 2000 is included in Appendix 2.

Host Plant Preference

To test for ant host preferences (Table 1; Figs. 1-2), we will first create an inclusive list of all tree species from which the ants are foraging. This list may take several years to compile, depending on the rate that it acquires new species. To evaluate the hypotheses that ants forage with either a fixed species rank preference (H_{1a}) (Table 1), or because of habituation (H_{1c}) (Fig. 2), leaves from each of the trees on the foraging list will be placed on 3 active trails per colony. Leaves will be placed on a random position on the path, one species at a time. Observers will then record the numbers of discs cut from each leaf in 15 min. Three replicate leaves of each species will be introduced and the order of introduction among species will be random, with at least 30 minutes between introductions. An ANOVA will be used to analyze differences in discs cut among tree species across all trails and colonies. To test our hypothesis related to a toxicity threshold (H_{1b}) all trees within a circle surrounding each focal mound (radius = length of longest harvest trail) will be surveyed, and the relative abundance of each tree species within that area calculated. These relative abundances will be compared to the ant preference test (Table 1).

Sustainability of Harvesting

To evaluate whether or not ants are harvesting tree resources sustainably, we will test for systematic changes in trail length with a general linear model that includes year and mound size, and uses the number of workers in a colony as a covariate. We will use measurements of average trail length (as defined in Baseline Data) and colony size. To measure colony size, we will count the number of workers per meter of trail. If ants do not harvest sustainably, we expect that trail length will increase from one year to the next (Fig. 3), and that the probability of mortality will be increase as trails lengthen (Fig. 4). If ants do harvest sustainably, we expect to see no change in average trail length over time.

Time Schedule of Data Collection

	Years of Data Collection
Baseline Data	All
Host Plant Preference	3 – 10 *
Sustainability of Harvesting	3 – 10 *

* or until the study is completed.

Literature Cited

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Appendix 1. Data sheet used in 2000.

Date: Nest Code: (S/P, Nest#)

Time: Nest Length: (m)
Group: Nest Width: (m)
#Active Entrances:

#Other Entrances:

Tree Code: (Nest Code, Tree#)	Entrance #	Trail Dist. (E-T) (m)	Items/tree	#	DBH (cm)	Tree Description
			Fresh Leaf Dead Leaf Flower Fruit/Seed Other			

Tree Code: (Nest Code, Tree#)	Entrance #	Trail Dist. (E-T) (m)	Items/tree	#	DBH (cm)	Tree Description
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			Fresh Leaf Dead Leaf Flower Fruit/Seed Other			

Date:
Time:
Point

Map Key
R = Reference Tree F = Focal
E = Entrance T = Tree

Nest Code	Entrance #	Bearing F-E	Dist. F-E (m)

Nest Code	Tree Code	Bearing F-T	Dist. F-T (m)

Appendix 2. Preliminary Data collected on 2 February 2000. Trail length distances (as the ant walks, or as the bird flies to hole or focal point) do not correspond by row due to unclear records.

Colony ID	Forest Age	Nest Length	Nest Width	Nest Area	No.Active Holes	No.Other Holes	Distance Ant Travels from Tree to Hole (m)	Distance bird flies from Tree to Hole	Distance from Tree to Focal Point	dbh Harvest Tree	Morphospecies	Buttress?
A	S	15.27	4.6	70.2	4	13	11.5		17.4	31	5	Y
							8.4		6.4	61	6	Y
							6.2		10.1	40.1	7	Y
							12.6		9.6	46.3	8	N
							61.6		61.6	73.2	9	Y
							105.3		40.5	33.4	10	Y
							84		22.4	130.5	11	Y
							132.6			42.5	7	Y
B	S	11.4	7.2	82.1	5	60	33.8	28.6		13.6	1	N
							100.1	132.6		25.5	4	Y
							80.6	130.3		21.5	1	N
							39	39		15.8	1	N
							41.6	40.3		51.5	4	Y
							45.5	42.9		2	1	N
							51.4	13.9		33.6	12	N
B	P	16.06	4.38	70.3	1	12				57	15	Y
								22				
								4		85.9	16	Y
								52.6		127.3	14	Y
								69.7		49.3	13	Y
A	P	12.7	5.25	66.7	4	6	6.4		7.4	110	10	Y
							2.5		12.5	33	11	N
							16.5		7.9	11	12	N
							12.7		29	29.9211293	9	N
							7.6		15.6	45.20000384	11	N
							0.3		31.9	41.3802852	11	N
							29.2		44	63.66197724	10	Y
							11.4		57	28.64788976	11	N
							31.8		8.75	19.09859317	11	N
							45.7		4.3	35.33239737	11	N
							62.2		19.2	32.46760839	9	N
C	P	28.8	6.4	184	2	8	3.4			31.12	18	N
							37			25	17	N
							40			5	17	N
							58			0	17	N
							48			155	17	N